

Natural History of Insects Living in Inflorescences of Two Species of *Heliconia*

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Abstract: The life histories of eight species of insects which live in the water-filled bracts of *Heliconia wagneriana* and *H. imbricata* are studied. Development times of larval forms are directly correlated with the length of time an inflorescence survives on a plant. Few predators were collected from these inflorescences. It is hypothesized that low predation rates may be important in the evolution of insects living in *Heliconia* inflorescences.

INTRODUCTION

Lowland Costa Rican rainforests contain a variety of plants in the genus *Heliconia* (Musaceae or Heliconiaceae of Smith, 1966). These plants show considerable variations in morphology, size, pollination systems, and habitat preference (Linhart, 1973; Stiles, 1975). Many *Heliconia* species have erect inflorescences which consist of a series of large bracts, each bract containing several flowers. These erect bracts collect and hold water from both rains and transportation processes. Such water-filled bracts of *Heliconia* serve as small aquatic habitats for a variety of organisms. Species of *Paramecium* are common in inflorescences of some *Heliconia* species (Vandermeer et al., 1972). Maguire,

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Belk, and Wells (1968) have shown that protozoan communities in *Heliconia* inflorescences may be fed upon by mosquitoes. This report examines the life histories of the most common insects, excluding mosquitoes, living in the inflorescences of *Heliconia wagneriana* Peters and *Heliconia imbricata* (Kuntze) found on Península de Osa, Costa Rica.

FIELD SITE AND NATURAL HISTORY *HELICONIA* SPECIES

This research was done within a 12 km radius of the Tropical Science Center Field Station near Rincón de Osa, Península de Osa on the Pacific coast of Costa Rica. This is an area of tropical wet forest, the climate, topography, and flora of which have been described by Holdridge et al. (1971). A dry season at the Península de Osa occurs from January through April.

On the Península de Osa, flower buds of *H. wagneriana* begin emerging at the end of December and flowering occurs for the population regularly throughout the dry season until late April. A mature inflorescence has between 4 and 8 pairs of bracts, each bract on an alternate side of the rachis. The length of the water containing portion of the bract is between 55 and 70 mm although an entire bract including the extending tip may be 20 cm. Bract widths are between 24 and 40 mm and the depths between 55 and 65 mm. The bracts contain as much as 6 cc of water. Although this plant grows in the dry season, the bracts are almost always filled with water. Most of the water apparently is the result of plant transportation processes. The only bracts of *H. wagneriana* which we have seen devoid of water (or with little water) have been those located in a single well drained and always sunny (12 hours a day in the dry season) area next to Aeropuerto Rincón. These inflorescences did not contain many insects. Remaining plants at this field site always held water and maintained an insect community.

H. wagneriana grows in relatively sunny areas in forest edges, along road cuts and along stream beds. When flowering, plants produce a new bract pair about each 9 days. Each inflorescence remains on the plant for about 11 weeks and shows little evidence of rotting until senescence.

Heliconia imbricata blooms during the rainy season from June through September. In contrast to *H. wagneriana*, most plants flower synchronously at the beginning of June with only a few inflorescences beginning after that time. At any given time, most of the inflorescences in a locality are of the same age. Inflorescences last on each plant for up to 11 weeks; however, by the eighth week nearly one-half of each inflorescence has rotted. This is again in contrast to *H. wagneriana* whose inflorescences maintain a constant state until shortly before they die. Flowering *H. imbricata* plants produce a new bract pair about once each week.

H. imbricata has small bracts, the lengths of which are between 50 to 70 mm, the widths between 25 and 35 mm and the depths about 30 mm. The water

held in these bracts although not measured, is considerably less than that held by *H. wagneriana*. Mature *H. imbricata* inflorescences carry between 8 and 14 pairs of imbricate bracts. This plant is found along streams or near treefalls (open areas in the forest caused by the death and subsequent falling of a tree) in more shaded areas in the forest. Within the study area, *H. imbricata* was encountered more frequently than *H. wagneriana*. Further information on the gross morphology of these and other *Heliconia* species is available (Smith, 1966; Stiles, 1975).

NATURAL HISTORY OF THE INQUILINE INSECT SPECIES

The life histories of 8 of the common species of insects living in *Heliconia imbricata* and *Heliconia wagneriana* inflorescences were studied in detail. These insects include 6 species whose interactions have been considered elsewhere (Seifert and Seifert, 1976). Observational studies on living clumps of *Heliconia* inflorescences yielded times and location of foraging, oviposition, and movements of the inquiline insects. The length of life cycles of some of the insect species was estimated by culturing insects in the field station.

Population densities of some insect species varied with inflorescence size and season. Several times a month, clumps of inflorescences were located, inflorescences were measured by number of bract pairs, and inflorescences were cut (Seifert, 1975). Each inflorescence was then dissected and the densities of insect species were recorded. Inflorescences were grouped together by number of bracts and separated by months. A Kruskal-Wallis nonparametric analysis of variance was used to determine if the density of each species of insect varied among months. *H. wagneriana* inflorescences ranging in size from 3 through 4 bract pairs and *H. imbricata* inflorescences ranging in size from 5 through 7½ bract pairs were used for this analysis. Both of these classes consisted of ⅓ of all possible size classes. Table 1 lists the median and range of numbers of individual insects per inflorescence by month as well as the *H* value (the Kruskal-Wallis statistic) for each species under study. From that table it can be seen that *Copestylum ernesta*, *Beebeomyia* sp., and *Odontolinus fasciatus* exhibit significant seasonal variation in *H. wagneriana* and that *Quichuana aurata* and *Cephaloleia puncticollis* exhibit seasonal variation in *H. imbricata*.

Litopeltis sp. (Dictyoptera: Blattidae). Nymphs of this cockroach were found in the inflorescences and occasionally in the leaves of *H. imbricata*. Individuals rest during the day within the bracts but forage at night both on the outer and inner surfaces of the bracts, feeding on decaying bract parts and mold growing on the bract tips. *Oothecae* were never found in the inflorescences and thus the length of developmental period was not measured. A Kruskal-Wallis test shows no significant differences of densities among the months tested.

TABLE 1. Median and range of numbers of individual insects per *Heliconia* inflorescence in each of three months.

		June	July	Aug.	<i>H</i>
<i>H. imbricata</i>					
<i>Quichuana aurata</i>	Median	20	2	0	22.286***
	Range	36	32	56	
<i>Gillisia</i> sp. #1	Median	2	2.5	1.5	1.242 ns
	Range	8	8	10	
<i>Merosargus</i> sp.	Median	4	8	4	1.147 ns
	Range	18	40	15	
<i>Cephaloleia puncticollis</i>	Median	12.5	8	4	8.994*
	Range	23	31	17	
<i>Litopeltis</i> sp.	Median	1	2	0	1.364 ns
	Range	15	18	18	
<i>Odontolinus fasciatus</i>	Median	0	0.5	0	1.617 ns
	Range	4	4	3	
<i>Beebeomyia</i> sp.	Median	0	1	0.5	1.844 ns
	Range	10	17	4	
		Jan.	Feb.	March	<i>H</i>
<i>H. wagneriana</i>					
<i>Quichuana aurata</i>	Median	23.5	25	23	1.912 ns
	Range	60	155	47	
<i>Gillisia</i> sp. #1	Median	2.5	3	10	5.521 ns
	Range	16	25	28	
<i>Copestylum ernesta</i>	Median	1	3	9.5	11.427***
	Range	7	27	26	
<i>Beebeomyia</i> sp.	Median	0	1	2	17.771***
	Range	1	10	16	
<i>Odontolinus fasciatus</i>	Median	0	0	2.5	17.427***
	Range	1	1	9	

Note: The differences in location among ranked counts are tested by the Kruskal-Wallis test, whose adjusted test statistic, *H*, is given in the last column. Statistical significance is indicated as follows: ns = $P > .05$, * = $.05 > P > .01$, ** = $.01 > P > .001$, *** = $P < .001$.

Cephaloleia puncticollis Baly (Coleoptera: Chrysomelidae; Hispinae). This is one of a number of hispine beetles which forage exclusively in *Heliconia*. Unlike most members of this subfamily, which feed on the cylindrically rolled new leaves of a species of *Heliconia*, larvae of this species feed on *Heliconia imbricata* inflorescences and most oviposition occurs in June. Eggs are laid in clusters of from 1 to 6 on the inside of the bracts. Larvae feed by rasping the inside of the

bract and rarely the flower. The larval period lasts about 60 days; pupae are attached directly to the bract and eclose after about 15 days. Densities of *C. puncticollis* larvae varied among months (Table 1).

Gillisia sp. #1 (Coleoptera: Hydrophilidae). This species is the most common beetle found in *Heliconia* inflorescences. It is abundant as an adult in both *H. wagneriana* and *H. imbricata* although the larval forms have not been found. The adult feeds on floral parts by crawling down the outside of the flower into the water. As this is done, an air bubble is trapped on the ventral surface by the hydrofuge hairs. The air bubble aids in buoyancy (if the hydrophilid is dislodged from the flower underwater it quickly bounces to the surface) and may be useful in respiration (Lanciani, 1970). *Gillisia* has been observed remaining in the water for as long as 3½ minutes but most underwater forays are between 30 and 60 seconds. When not feeding, this beetle rests above the water on the inside of the bract near the rachis. Copulation, but not oviposition, has been observed in the inflorescences. Although we have not observed *Gillisia* larvae in these plants, P. J. Spangler has informed us that he has obtained a few *Gillisia* larvae from *Heliconia* inflorescences in Ecuador. The common occurrence of adult *Gillisia* in *Heliconia* and the rarity of their larvae in *Heliconia* lead us to believe the main larval habitats are not *Heliconia* inflorescences. Density variation of adults among months was not significant (Table 1). During the non-blooming season these beetles can be found in the young leaves of *Heliconia*.

Gillisia is a genus with few described members (P. J. Spangler, personal communication). A second species of *Gillisia* is found occasionally in these *Heliconia* inflorescences, and we have observed similar species in Venezuelan *Heliconia*.

Odontolinus fasciatus Sharp (Coleoptera: Staphylinidae). This beetle is occasionally found as an adult in both species of *Heliconia*. It walks down the flower or the inside of the bract into the water, captures mosquito larvae and returns above the water to devour them. It is not uncommon for *O. fasciatus* to continue foraging until several mosquito larvae have been eaten. Laboratory observations indicate that this staphylinid will eat newly emerged larvae of the flies *Quichuana aurata* and *Beebeomyia*, both of which are common in these *Heliconia*. However, newly emerged larvae of these fly species are usually found in bracts which are only very slightly open and which would be difficult for *Odontolinus fasciatus* to enter. Population densities of *O. fasciatus* vary among months in *H. wagneriana*. *O. fasciatus* is infrequently found in *H. imbricata* (Table 1).

Quichuana aurata Walker (= *Q. picadoi* Knab in Seifert and Seifert, 1976). This insect is found in both *H. wagneriana* and *H. imbricata*. Oviposition occurs throughout the flowering season of *H. wagneriana*. Females choose as an oviposition site bracts which are slightly opened. The female lands and extends

a three pronged ovipositor into the inside of the bract. A female will reject a bract if previous eggs have been laid there (including both hatched and unhatched eggs) although she may oviposit in several inflorescences in a single clump. The number of eggs laid in one clutch ranges from 8 to 32. *Q. aurata* lays eggs in *H. wagneriana* from January to April, as successive bracts develop throughout this period. Due to the continual oviposition by adults on the young bracts, several larval size classes, ranging from newly hatched to last instar can be found in a single inflorescence. Larvae hatch 2 days after oviposition and feed for about 45 days on floral parts, nectar, and detritus on the floor of the bract. Larval densities show no significant difference among months in *H. wagneriana* (Table 1).

Pupal life lasts about 8 days and eclosion has only been observed in the morning. Laboratory work has shown that if newly emerged flies are not allowed to dry their wings immediately after eclosion, they will be unable to fly. The morning eclosion of *Q. aurata* pupae is probably a response to afternoon rains in the wet season.

The natural history of *Q. aurata* is somewhat different in *H. imbricata*. Oviposition on *H. imbricata* occurs only when the inflorescence is a small bud and primarily during the beginning of the flowering season. This may be due to the relatively quick rotting of *H. imbricata* inflorescences. Correspondingly, densities of *Q. aurata* vary among months in *H. imbricata* (Table 1).

The larval food sources of *Q. aurata* are the inflorescences of *Heliconia wagneriana* and *H. imbricata*. We did not find *Quichuana* larvae in non-*Heliconia* water-filled plants (such as bromeliads) on the Peninsula de Osa. Hence, there appear to be 6 months during each year (May and August through December) when populations of this insect consist entirely of adults. However, when *H. wagneriana* begins to bloom in January, the larval populations are as high as later in the season (Table 1), when reproduction from adults which matured in the previous month occurs, and when adult populations should be at their highest. Since no change in larval densities of *Q. aurata* occurs in *H. wagneriana*, the adult population is presumably large enough to maintain the larval population at maximum densities throughout the year.

A second morphological form (provisional number 7627 of F. C. Thompson) of *Quichuana* exists in these Costa Rican *Heliconia*. The morphological structure of the adults of *Q. aurata* and the second form are identical except that *Q. aurata* exhibits bright golden metallic pile on the body while the pile from the second form is grey. (The taxonomic status of this form will be discussed by F. C. Thompson.)

Larvae of *Q. aurata* are occasionally found in a third species of *Heliconia*, *H. latispatha* Benth. on the Peninsula de Osa. In the laboratory, we have reared larvae to adults feeding them only *H. latispatha*. However, in the field only one pupa of *Quichuana* has been found in this species of *Heliconia*. Skutch found

TABLE 2. Summary of natural histories of common insect species inhabiting two species of *Heliconia* inflorescences.

Insect species	<i>Heliconia</i> sp. inhabited	Insect stage	Food	Oviposition site	Developmental period	Dependency on <i>Heliconia</i> inflorescences
<i>Litopeltis</i> sp.	<i>imbricata</i>	nymph	outside of bracts	unknown	unknown	great
<i>Cephaloleia puncticollis</i>	<i>imbricata</i>	larva	inside of bracts	bracts	75 days	great
<i>Gillissus</i> sp. #1	<i>wagneriana imbricata</i>	adult	detritus, flower parts	unknown	unknown	great
<i>Odontolinus fasciatus</i>	<i>wagneriana imbricata</i>	adult	mosquito larvae	unknown	unknown	some
<i>Quichuana aurata</i>	<i>wagneriana imbricata</i>	larva	flower parts, detritus, nectar	bract tip	55 days	great
<i>Copestylum ernesta</i>	<i>wagneriana</i>	larva	flower parts, nectar	flowers	60 days	great
<i>Merosargus</i> sp.	<i>imbricata</i>	larva	flower parts, rotting flower parts, detritus	rachis	70 days	great
<i>Beebeomyia</i> sp.	<i>wagneriana imbricata</i>	larva	flower parts	rachis	unknown	unknown

Eristalis (probably *Quichuana*) in *H. bihai* L. (= *wagneriana*) in Panama (1933) and has noted its presence in Costa Rica (1971). We have seen *Quichuana* larvae in Colombian and Venezuelan species of *Heliconia*, and similar species have been found sporadically in Jamaican bromeliads (Laessle, 1961).

Copestylum ernesta (Curran) [= *C. cf. obscurior* (Curran) in Seifert and Seifert, 1976] (Diptera: Syrphidae). This fly breeds almost entirely in *H. wagneriana*. Maturation from small larvae to adults requires 50 to 60 days and larval densities greatly increase from January to March (Table 1). Foraging habitats include nectar feeding and consumption of detritus. Since this organism is found only rarely in *H. imbricata*, this fly either lives as an adult from May through December or as larvae on other resources during that period.

Merosargus sp. (Diptera: Stratiomyidae). This undescribed species of *Merosargus* is abundant in *Heliconia imbricata* but absent from *H. wagneriana*. Copulating pairs of adults are seen resting on *Heliconia* leaves or on vines, stems, or other parts of plants near *Heliconia* clumps. Eggs are laid on the rachis below the lowest bract. The leathery larvae feed on rotting floral parts and detritus and maturation from egg to adult takes from 60 to 70 days. Densities in small inflorescences do not change during the months of *H. imbricata* flowering (Table 1). Since *Merosargus* larvae are abundant in *H. imbricata* but absent from other environments examined, including non-*Heliconia* habitats, it is possible that an adult population is maintained for 8 months between reproductive periods. (M. T. James will describe this species.)

In *H. wagneriana*, the congener, *M. gowdeyi* Curran is occasionally found. The adults of this *Merosargus* are commonly seen courting and copulating near various species of *Heliconia*, but the larvae may be more closely associated with *H. latispatha* than with either of the species of *Heliconia* under study.

Beebeomyia sp. (Diptera: Richardiidae). *Beebeomyia* larvae feed on both *H. imbricata* and *H. wagneriana*. Flower parts, particularly the petals, and nectar seem to be the main food source. Oviposition occurs on the rachis or inside the bract near the juncture of the rachis and bract. Larvae occasionally are found in *H. latispatha* and adults are seen copulating there as well as near *H. imbricata* and *H. wagneriana*. Densities increase from January to March in *H. wagneriana* but remain constant in *H. imbricata*. The development time was not measured. (B. Steyskal will describe this species.)

Table 2 presents a summary of the natural histories of the insects under study.

DISCUSSION

Few organisms prey on insects which live in *Heliconia* inflorescences. One insect not discussed above, the earwig *Carcinophora americana* (Beauvois) (Dermaptera: Carcinophoridae) is found rarely in *Heliconia* inflorescences.

Adults of this species have been maintained in the field station for over 3 months and will feed on most insect species found in the inflorescences. Thus, a single inflorescence could support an adult *C. americana* for at least several weeks. However, this earwig occurs so infrequently in the inflorescences that it is unlikely to be an important predator. In the field station, the staphylinid beetle, *Odontolinus fasciatus* (Sharp), has been seen to feed only on mosquitoes. We have occasionally seen spiders waiting on the edges of the bracts and capturing adult *Quichuana aurata*. Similarly, one anole was seen feeding on an adult *Q. aurata*. Predation does not seem to be important in the natural history of these insects while they live in the inflorescences. The relative low importance of predation has been noted in mosquito populations living in pitcher plants (Istock et al., 1975) as well as among hispine beetles living in *Heliconia* leaves (D. R. Strong, personal communication).

That this system is largely predator free may be important in the evolution of these insect species. Insects which live as larvae in *Heliconia* inflorescences have larval and pupal stages that are close to the length of time that each inflorescence survives. The length of development time of *Cephaloleia puncticollis* is between one and two weeks less than the length of time that *H. imbricata* inflorescences go from bud to complete rotting. Pupae of this species are often found in inflorescences in which substantial rotting has occurred. *Merosargus* sp. larvae and pupae spend nearly as much time in the inflorescences as do larvae of *C. puncticollis*. Development times of *Q. aurata* seem to be geared to the time at which *H. imbricata* begins to rot, rather than the complete rotting of the inflorescence.

Larval forms can maintain themselves in the bracts no longer than the time from bud emergence to flower rotting. Selection must favor eclosion to adult forms before the death of the inflorescence. As Williams (1966) has pointed out, selection could initially favor organisms which reproduce as quickly as possible. Typically, selection on energetic constraints limits reproduction so that reproduction occurs when the probability of success is maximized. Reproductive success of insects in *Heliconia* inflorescences may involve maximizing the amount of time larvae stay in inflorescences. Low levels of predation in inflorescences may allow larvae long development times, particularly if adult forms or forms moving between inflorescences are subjected to high mortality. Decreasing development time would not be an optimal strategy. For insects living in *H. imbricata*, individuals which emerge midway through the life of an inflorescence would be exposed to an environment in which most of the inflorescences are relatively old. In such a case, rotting of the inflorescence would occur before complete development of the insects. Alternatively, extending the development time in a predator free habitat, such as the inflorescences, would lead to greater probability of survival until the next blooming season and a subsequent greater probability of a reproductive success. Thus, selection maximizing time spent in

an inflorescence may occur for insects in *H. imbricata* inflorescences. Since *H. wagneriana* blooming is much more staggered temporally than is *H. imbricata* blooming, adults emerging from *H. wagneriana* inflorescences often will be able to find young inflorescences for oviposition. Maximizing life time in the inflorescence may be a response to selection pressures primarily associated with *H. imbricata*. Counteracting selection pressures occur for insects living in *Heliconia* inflorescences: selection to maximize development time will be counteracted by selection to reduce development time to coincide with the length of life of the inflorescence.

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